

TAXONOMIC AND MORPHOLOGICAL STUDIES ON
THE ENCHYTRAEIDAE OF ILLINOIS

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY

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INTRODUCTION.

But very little work has been done on the Enchytraeidae in North America and that has been confined to restricted and widely separated localities. Aside from the description of *Fridericia agilis* Smith, nothing has been done in this field in Illinois. A striking contrast is thus offered with the condition in Europe where the field is well worked and the literature is becoming quite extensive. The writer has undertaken some investigations in this field in Illinois and the following paper represents some of the results of this study and is offered as a thesis in partial fulfillment of the requirements for the degree of Master of Arts.

The writer wishes to express his indebtedness to Professor Frank Smith under whose direction this work was done and who rendered valuable assistance from time to time during the progress of the work. Acknowledgments are also due to Dr. J. Percy Moore for his kindness in supplying type material of *Fridericia longa* and cotype material of *Fridericia agricola*; Mr. James Zetek for material supplied; and the Illinois State Laboratory of Natural History for the use of valuable works from its library.

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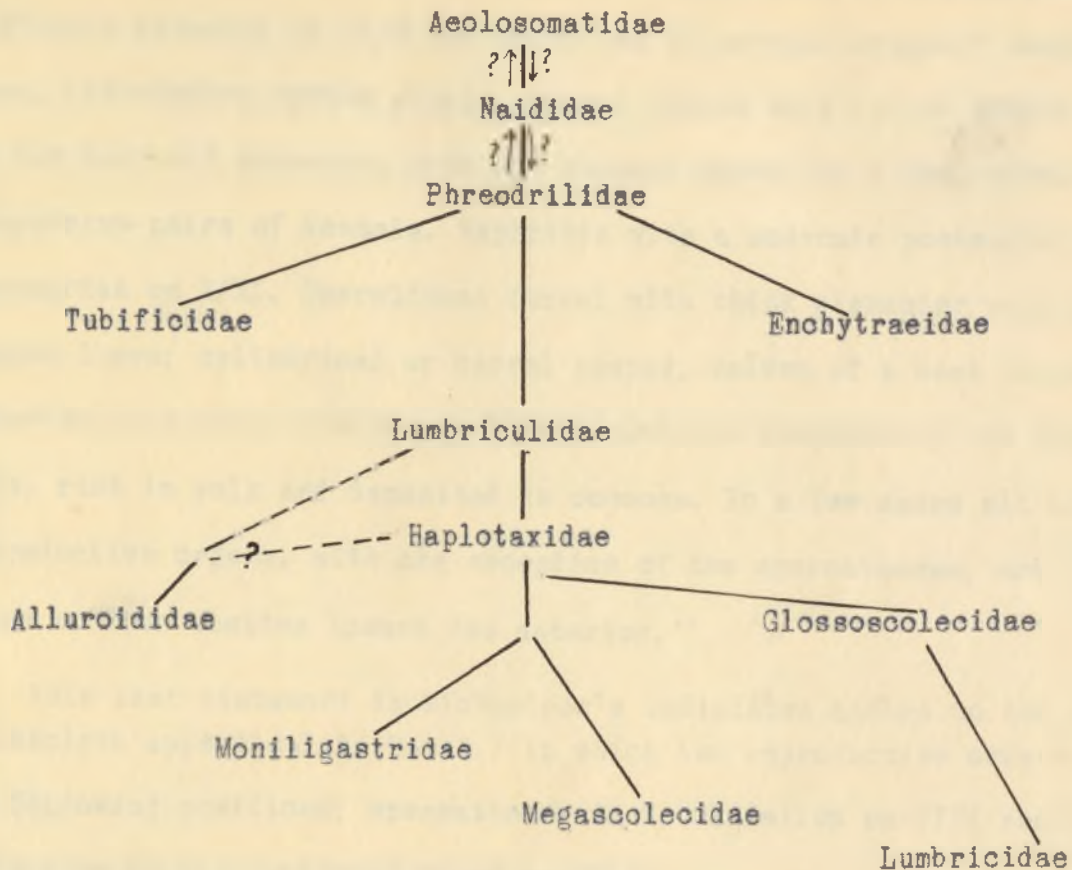
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FAMILY ENCHYTRAEIDAE.

This family is represented by a large number of species distributed among fourteen genera. They are wide spread in their distribution, being common in all parts of the American continent, generally distributed in Europe, and reported from Siberia, New Zealand and North Africa. They are found in a wide variety of situations. Some are aquatic, many terrestrial, and some are reported as being common to either kind of situation. Marine forms are also common. All are small in size, seldom exceeding 35 mm. They are, in some respects, quite similar to the earth worms; viz., (1) the setae are simple; (2) the wide separation of the spermathecae from the spermiducal pores; and (3) the presence of paired or unpaired glands comparable to the calciferous glands of the earthworms; and (4) the thick body wall. In other respects they resemble the lower Oligochaetes; viz., (1) the presence of numerous lymphocytes in the coelomic fluid; (2) the sperm ducts are confined to two somites, one of which contains the internal opening and the other the external opening; (3) the oviduct is reduced to a mere pore. Several of the important systematic characters of this family are based on internal structures which are subject to a rather wide variation.

The systematic relations of this family to the others is given by Michaelsen ('03, p.37) as follows:



DEFINITION OF THE FAMILY ENCHYTRAEIDAE:

"Setae (absent in Anachaeta) not bifid at the extremity; without distinct nodulus; straight or feebly bent in the shape of an S; usually three to twelve in a fan shaped bundle; seldom two, one or entirely wanting. Head pore present. Nephridial pores anterior to the ventral setae bundles. Clitellum on XII and on more or less greater part of the adjacent somites. One pair of spermiducal pores on XII in front of the ventral setae bundles. Usually one pair of spermathecal pores, inter-segmental in position, between IV and V; occasionally two pairs, inter-segmental in position, between III and IV, and IV and V. Alimentary canal

* Translated from Michaelsen ('00, p. 66).

with dorsal pharynx through which the several pairs of septal glands, beginning anterior to IV/V and occurring in several adjacent somites, open. Circulatory system simple; dorsal vessel only in the anterior part of the body and connected with the ventral vessel by a few, usually three, transverse pairs of vessels. Nephridia with a moderate postseptal region. Spermaries on X/XI. Spermiducal funnel with thick glandular wall and a narrow lumen; cylindrical or barrel shaped, seldom of a bent funnel shape; anterior to XI/XII. Ovaries on XI/XII. Oviduct rudimentary, on XII/XIII. Eggs, rich in yolk and deposited in cocoons. In a few cases all of the reproductive organs, with the exception of the spermathecae, are displaced three or four somites toward the anterior."

This last statement in Michaelsen's definition refers to one species (*Buchholzia appendiculata* Buchh.) in which the reproductive organs have the following positions: spermathecae in V; Clitellum on VIII and IX; spermaries in VII; oviducal pores in (?)IX.

Somewhat recently two new species have been described which are noteworthy in this connection. Stephenson ('09, p.109) has described *Fridericia stewarti*, a form from Tibet, in which the reproductive organs seem to occupy rather unusual positions. His description of the sexual organs is incomplete but he figures a developing sperm mass in X and ova and yolk in XI. In the description of *Fridericia californica*, Eisen('04, p.119) makes the following statement: "Ovaries extend as far back as XV and XVI!" If the above mentioned species have been accurately described, it is evident that the definition for the family Enchytraeidae must be modified so as to provide for these variations. However, until more is known concerning these two species, it seems best to allow the definition of the family to stand as given above and to pass this apparent discrepancy without further comment.

GENUS FRIDERICIA.

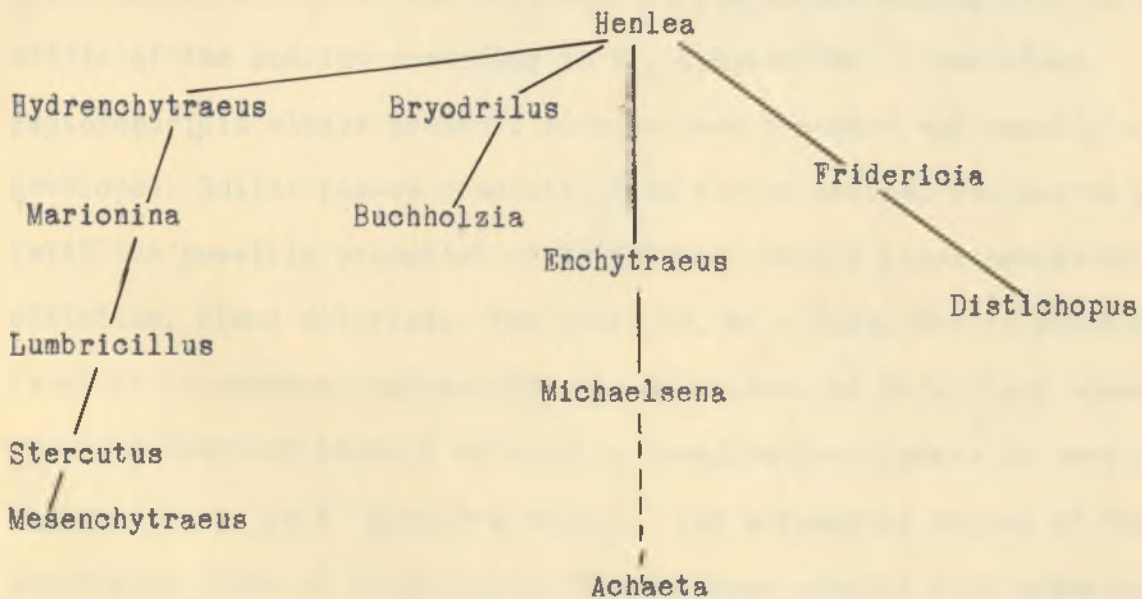
This is a relatively distinct genus. The chief characters which separate it from the other genera are: (1) the dorsal pores which are not found in any other Enchytraeid genus with the possible exception of *Enchytraeus humiculator* Vejd.; and (2) the development and arrangement of the setae. They are produced in each bundle two at a time, the outer pair constituting the oldest and largest ones. The next pair lies immediately within the oldest, the next in age within these and all others following in the same order. The group thus formed is fan shaped, with a pair of outer, large setae and possibly gradating pairs between. Sometimes an old seta may fall out thus destroying the symmetry.

Fridericia is the largest genus of the family Enchytraeidae. Michaelsen ('00, p. 94) allowed twenty one species. Since that date the number has increased considerably and at present there are sixty six apparently good species recognized, besides three doubtful ones. Of the sixty nine(?) species of Fridericia, fourteen have been described from North America. They are as follows:

<u>Name</u>	<u>Type Locality</u>
<i>F. alba</i> Moore	Philadelphia, Penn.
<i>F. agricola</i> Moore	Philadelphia, Penn.
<i>F. longa</i> Moore	Philadelphia, Penn.
<i>F. agilis</i> Smith	Havana, Ill.
<i>F. harrimani</i> Eisen	Mountain View, Cal.
<i>F. johnsoni</i> Eisen	Santa Barbara, Cal.
<i>F. fuchsi</i> Eisen	Santa Cruz Mts. near Boulder Creek, Cal.
<i>F. sonorae</i> Eisen	Sonora, Mexico.
<i>F. santaerosae</i> Eisen	Santa Rosa, Sonoma Co. Cal.

<u>Name</u>	<u>Type locality</u>
<i>F. santaebarae</i> Eisen	Santa Barbara, Cal.
<i>F. popofiana</i> Eisen	Popof Island, Alaska.
<i>F. macgregori</i> Eisen	Napa Co. Cal.
<i>F. californica</i> Eisen	San Francisco, Cal.
<i>F. parva</i> Moore.(?)	Philadelphia, Penn.

The systematic relations of this genus to the other thirteen genera of the family is given by Michaelsen ('03, p.52) as follows:-



Recently Cejka ('10, p.1) has described a new genus, *Hepatogaster*, from material collected in New Siberia Island. Cejka states that this new genus is closely related to *Henlea* and *Buchholzia*.

The genus *Chirodrilus* Verrill has been the subject of much dispute. Both Vejdovsky and Vaillant placed it among the Tubificidae while Beddard ('95, p.314) and Michaelsen ('00, p.88) placed it among the Enchytraeidae. Later Michaelsen ('03, p.50) placed it among the Tubificidae.

There seems to be good grounds for considering it as a Tubificoid genus and it seems wise to omit it here.

GENUS FRIDERICIA MICHLSEN.*

Definition: Setae straight, at most with a short hook shaped bend at the proximal end; the bundles consist either constantly of two equally large setae or a larger number of which those toward the middle of the bundle are noticeably reduced in length and thickness. Head pore small, in the dorsal medial line on O/I. Large dorsal pores, surrounded by hypodermal guard cells, perforate the body wall in the dorsal median line in the middle of the somites posterior to VI. Lymphocytes of two kinds. Peptonephridia always present, more or less branched and usually strongly developed. Gullet passes gradually into the intestine. The dorsal vessel (with the possible exception of *F. perrieri* Vejd.) rises posterior to the clitellum. Blood colorless. The brain is, as a rule, convex posteriorly (when it is concave posteriorly, the neurilemma at this place shows a strong thickening through which this invagination appears to have arisen abnormally, as in *F. lobifera* Vejd.). The anteseptal region of the nephridium tends to be globular. Spermathecae usually with spherioal diverticula!'

TECHNIQUE.

The following are the methods used in the preparation of the material for this investigation.

The worms were gradually anesthetized by means of chlorotone of about five percent strength. They were then straightened and treated with

* Translated from Michaelsen ('89, p. 40).

Gilson's fluid or with concentrated corrosive sublimate solution.

Specimens were imbedded in paraffin and cut 10 microns thick. A few sections were cut 7 microns thick in order to show some of the finer histological detail. Sections were made in the three principal planes.

Any of the general stains used were found to yield good results but most of the sections were treated with Ehrlich's haematoxylin and eosin which proved very satisfactory.

A number of points of the gross anatomy were worked out by means of dissections made under a Zeiss Binocular dissecting microscope. This method was found to be particularly useful in determining the characters of the spermathecae, sperm duct, and the brain.

Drawings were made by the aid of a Zeiss-Abbe camera lucida. A number of points were worked out by means of reconstructions and composite drawings from camera lucida sketches. The magnification is indicated on each drawing.

DESCRIPTION OF FRIDERICIA FIRMA NOV. SP.

Definition.

Length 24-33mm. Somites about 64 (extremes 62-67). Color whitish yellow. Prostomium blunt. Dorsal pores begin in VII. Setae of unequal length, the inner ones being shorter; 4-7 setae in the anterior bundles, 4-5 in the middle bundles, and 2 in the posterior bundles. Head pore at O/I. Clitellum on XII and XIII. Septal glands in IV, V, and VI. Peptonephridia branching dendritically. Brain $\frac{1}{4}$ longer than wide; posterior margin convex, anterior margin concave. Dorsal vessel rises posterior to the clitellum. Commencing with VII, the intestine is covered with numerous, somewhat rectangular chloragog cells. Spermathecae with pear shaped ampullae connecting with the intestine in V and each bearing

at its base three to four sessile, unequal, lobe-like diverticula.; duct longer than the ampulla, is cylindrical, slender and without glands at the external opening. Anteseptal part of the nephridium slightly smaller than the postseptal part; the terminal duct rises from the anterior part of the latter and opens in front of the ventral setae. Length of the spermiducal-funnel $1 \frac{1}{3}$ times as great as its diameter; its duct is long, slender, much contorted and confined to XII. Lymphocytes elliptical.

The characters of the penial bulb and the chylus cells, which according to Eisen present constant generic and specific differences, will be taken up and discussed at length in a later part of the paper.

The specimens of this species were found in woods near Urbana, Illinois, in rich soil and under decaying leaves in undisturbed forest land. Specimens were found sexually mature in November.

Affinities of *F. firma* nov. sp.

This species is easily separated from the closely related species; viz., *F. agilis* Smith; *F. longa* Moore; and *F. ratzei* Eisen. The following table indicates the resemblances and differences of these species.

	<i>F. firma</i> nov. sp.	<i>F. agilis</i> Smith	<i>F. longa</i> Moore	<i>F. ratzeli</i> Eis
Length	24-33 mm.	25-30 mm.	25-30 mm.	16-30 mm.
Somites	62-67.	57-66	60-69.	45-60.
Setae	In anterior region, 4-7; in middle region, 4-5; in posterior, 2.	Usually 2; occasion- ally 4.	In anterior region, 4; in posterior, 2.	In anterior 6-8. ..posterior 4.
Peptonephridia	Dendritically branch- ed; open in IV very close to septum III/IV.	Large, much branched open in III very close to septum III/IV.	Bag shaped; unbranch- ed; open in V.	Repeatedly branched.
Brain	1/4 longer than wide; anterior moderately concave; posterior quite convex.	1/2 longer than wide; anterior slightly concave; posterior quite convex.	Somewhat longer than wide; posterior convex.	A little longer than wide; ant. and post. convex.
Spermathecae	With 2-3 sessile, unequal, lobelike diverticula; no glands at external opening.	With about 9 well developed diverticulae; no glands at external opening	With 5-8 diverticula; unicellular glands at external opening.	With 6-8 small sack shaped diverticula; glands at external opening.
Nephridia	Anteseptal slightly smaller than postsep- tal. Duct rises from anterior part of latter.	Anteseptal= postsep- tal in size; duct rises from posterior part of latter.	not described.	Anteseptal large; duct rises from ant. part of post- septal.
Sperm ducts	Funnel 1 1/2 times longer than the diam- eter; duct slender, much coiled, and confined to XII.	Funnel 2 times as long as diameter; duct long, slender, much coiled, and confined to XII.	not described.	Funnel a little longer than diameter.

External Characters.

External appearance.

This species has a rather characteristic appearance. The surface is smooth, glistening, and firm to the touch. The body is long and slender. The length is about 30 mm., the extremes being 24-33. In a transverse section the body is circular in outline. The diameter is greatest in the region of the clitellum (0.6 mm.) and gradually decreases from that region anteriorly and posteriorly. The entire body is opaque, of a yellowish white color, and the exterior is characteristically glistening.

Metamerism.

Five body regions may be distinguished but the relative differentiation of each is not specially marked. These regions may be designated as; (1) anterior; (2) preclitellar; (3) clitellar; (4) postclitellar; and (5) anal. The intersegmental grooves are rather obscure except in a region just behind the prostomium where a few are quite distinct, but passing posteriorly, they gradually become shallow almost to disappearance. The external annulations correspond to the internal metamerism. No secondary annulations are present. The number of somites is not constant, the extremes being about 62-67 and the average about 64.

Cephalization.

The anterior region of the worms of this species presents no essential differences from that of the other allied species. The prostomium is blunt and rounded (Fig. 1, Pr). The anterior region is morphologically the specialized first somite which, as in ^{the} other species, does not bear setae. The two chief structures present are the ventrally directed mouth and the head pore (Fig. 4), the latter appearing as a narrow slit-like opening on the medial dorsal aspect on O/I.

Preclitellar region.

The preclitellar region begins with II and extends to XII. No special external differentiations are present in this region except the spermathecal pores.

Clitellar region.

The clitellum is on XII and XIII. Special differentiations in the form of two pairs of openings, viz., the spermiducal and the oviducal pores, are present on the ventral surface.

Postclitellar region.

The postclitellar region comprises the variable number of somites lying between the clitellum and the anal somite. No special external differentiations are present.

Anal region.

The anal region is the final somite of the body which bears the anus. It is differentiated only in that the transverse diameter is slightly greater than that of the region immediately preceding it.

External apertures..

The following openings are present: (1) mouth on I; (2) anus on the final somite of the body; (3) the single head pore on O/I; (4) median, unpaired dorsal pores beginning on VII; (5) the pair of spermathecal pores on the right and left sides of V; (6) the pair of spermiducal pores on the ventral side of XII; (7) the pair of oviducal pores on the ventral side of XIII; and (8) the external openings of the nephridia, a pair on each somite beginning with VII. With the exception of the mouth and the anus, all of these openings are small and inconspicuous, although the spermiducal pores in certain states of protrusion show distinctly under slight magnification.

Setae.

The setae have the typical *Fridericia* form and arrangement. The bundles are disposed, as usual, in four rows; viz., two lateral and two ventral. In each bundle the bases of the setae are in somewhat close approximation but are arranged in the transverse plane. Emerging from the body wall they spread out in the manner of fan rays (Fig. 2). Usually they are in pairs and each individual seta is bent slightly away from the other member of the pair. The number of setae range from 6-7 in the bundles in the anterior region of the body, to 4-2 in the posterior region. In the groups of more than two, the outer pair of setae are the largest and longest and represent the oldest setae of the bundle. The inner is always the smallest and shortest and represents the youngest setae. Between these two pairs there may occur a third pair which is transitional in length and size between the inner and outer pairs and are intermediate in age. Close examination shows that, strictly speaking, these setae do not occur in pairs since the members of the so called pairs are not equal in development but are only approximately so, one being slightly longer and more fully developed than the other (Fig. 2). This fact seems to indicate that the setae are developed one at a time and that no two setae of any one bundle coincide as to age. The proximal ends, especially of the more fully developed setae, are strongly bent (Fig. 3).

It will be noted that the above description conflicts slightly with the definition of the genus *Fridericia* which implies that the members of a so called pair are equal. However the description of the genus may stand unchanged since the members of the so called pairs, while not exactly equal, are approximately so and are distinct enough from the remaining setae of the bundle so that there is no danger of confusing the

components of one pair with those of another.

Internal Anatomy and Histology.

Body wall.

The body wall is composed of the usual four layers; viz., (1) cuticula; (2) hypodermis; (3) muscular layer; and (4) parietal epithelium.

Cuticula.

The cuticula forms an outer, complete envelope for the entire body. In this species it is tough and firm and presented the chief difficulty in the dissection of alcoholic specimens. When once broken it can easily be stripped from the body. It possesses a characteristic lustre, either in surface or sectional views, and gives the glistening appearance referred to previously. It is of about the same thickness throughout the length of the body. It is reflected into the mouth and lines the digestive canal as far as the openings of the peptonephridia in IV. It lines for a short distance the basal part of the lumen of the peptonephridia (Fig. 18, B.Pn). It is also reflected inward at the anal region and lines the intestine for about seven somites. It lines the channel of the head pore for most of its length (Fig. 4, Cu) but does not seem to line the channels of the dorsal pores (Fig. 5). It is reflected into the external opening of the spermathecal duct (Fig. 9, Cu) and lines its lumen from its beginning to its junction with the ampulla. It does not have any part in the structure of the oviducts (Fig. 26) being merely perforated at the oviducal pores. It lines the invagination of the body wall at the penial bulb region and lines the central chamber up to its junction with the sperm duct proper. The relatively small thickness of the cuticula can be attributed to the fact that this species lives in moist earth. According to Vejdovsky ('79, p.11) forms such as *Anachaeta*, which live in dry

surroundings have very thick cuticula, while those living in water or in very moist earth have a thin delicate cuticula. It was noticed in this species that the mortality was very high when the earth surrounding them approached dryness or when they were exposed for a short time to the air.

Hypodermis.

The hypodermis is an easily defined layer of cells in all parts of the body and is easily traceable over the exterior and into the mouth and anal openings. With the exception of certain modifications to be noted below, the hypodermis is made up of epithelial cells of the columnar type (Fig. 6, ep). Surface sections show that the nuclei are arranged in more or less definite transverse rows, indicating that the cells are similarly disposed. Unicellular glands are apparently absent. The hypodermis becomes considerably modified in the following regions: (1) prostomial; (2) clitellar; (3) anal. In the region of the prostomium it becomes greatly thickened. Beginning with the intersegmental groove I/II, it increases in thickness until it reaches a maximum at the anterior end of the prostomium (Fig. 13, Pr), attaining there a thickness 5-6 times greater than the usual one. It gradually becomes reduced in thickness as it is reflected back into the mouth to a nearly normal thickness. The cells of this region are about ten times longer than their transverse dimensions; are wider at the distal than at the proximal end, and are conspicuously nucleated. This thickening has very much the appearance of sensory epithelium.

On the anal somite the hypodermis is somewhat thickened, being about 2-2 1/2 times the normal thickness. However no apparent structural differences accompany this increase of thickness.

The clitellum occupies XII and XIII. Here the hypodermis is modified in a characteristic way, both in dimensions and in contents. It consists

of a single layer of cells which has increased in thickness, the maximum being about ten times the normal. This increased thickness is uniform throughout the circumference of the body except at the penial bulb invaginations where, at two latero-ventral areas, the clitellar hypodermis is interrupted. The cells are all similar in shape and contents. They are about five times as long as wide and polygonal in transverse section (Fig. 27, E). The nuclei are located uniformly at the bases of the cells. The cytoplasmic contents appear reticulated when stained and does not stain nearly so deeply as that of the hypodermis proper.

Muscular layer.

The muscles of the body wall present no significant departure from the condition described for other species of *Fridericia*. The circular muscle sheet (Fig. 6, cm), forming the layer which lies immediately below the hypodermis, represents about one sixth of the total muscular thickness and is composed of finely packed fibers. The longitudinal muscles are composed of two layers; viz., the ''röhrenförmige Längsmuskeln'' and the ''bandförmige Längsmuskeln''. These are represented in transverse section in figure 6, tu, lm.

Peritoneum.

The peritoneum (parietal) forms the innermost layer of the body wall (Fig. 6, P). It is characterized by its thinness, obscured cell boundaries, and conspicuous nuclei (in transverse section).

Coelom.

The coelom in this species conforms in most respects to that described for the other species of this genus. It is comparatively spacious and divided into compartments corresponding to the external metamerism. This division is effected by the septa which are developed in their usual

positions except in the first two or three somites where they are absent or obscured. It is lined everywhere by a peritoneum which differs in structure according to the region. The structure of the parietal layer and the peritoneal covering of the septa is as described previously. The splanchnic layer which covers the intestine presents the greatest modification. It is differentiated, chiefly in the intestinal region, to form the thick layer of cells described by Claparède as chloragog cells (Fig. 13,Cg). They first appear in the fifth somite and are present throughout the length of the intestine. These cells form a columnar epithelium, one cell thick, and are rounded at the distal ends. The contents of the cells are distinctive (Fig. 19,C). The cytoplasm is densely but finely granular and the nuclei are prominent. All of the organs lying in the coelomic cavity are enveloped in a layer of peritoneum similar in structure to the parietal layer except the gonads which are themselves proliferations of the peritoneum.

Elliptical lymphocytes (Fig. 11) occur in great abundance in the posterior somites but only a few are present anterior to the septal glands.

A number of foreign bodies were sometimes found in the coelomic cavity of the posterior half of the body (Fig. 12). The structure of these bodies seems to indicate that they are some form of protozoon parasite. No attempt has been made as yet to determine them.

The coelom is placed in communication with the external world by the head and dorsal pores, the nephridial pores, the spermiducal pores, and the oviducal pores. The last three sets of pores will be discussed later under their respective systems.

The first dorsal pore is in VII. Each pore occupies a median dorsal

position in the middle of each somite and is a perforation of the body wall, bordered by large, glandular cells.

The head pore is also a perforation of the body wall occupying a median dorsal position in O/I. Figure 4 shows the structure as exhibited in transverse section.

Digestive system.

The alimentary canal is a nearly straight tube extending from the mouth to the anus. It is differentiated into four regions, viz., (1) mouth and buccal cavity; (2) pharynx; (3) oesophagus; and (4) intestine (Fig. 13). These regions are easily defined except in the case of the oesophagus and the intestine where there is some difficulty in establishing the exact line of demarcation between the two.

Mouth and Buccal cavity.

The mouth (Fig. 13, m.) is a transverse opening, ventral in position, and borne on the first somite. It is overhung by the prostomium on the dorsal side. It opens immediately into the buccal cavity which constitutes the first region of the tract and extends to the beginning of the dorsal epithelial thickening which marks the anterior limit of the pharynx. The external cuticula is reflected into the mouth and lines the buccal cavity. This cuticula presents no modifications except for a slight diminution in thickness. Beneath it lies an epithelial layer which is one cell thick, conspicuously nucleated, and is a continuation of the external hypodermis. This epithelial layer has definite thickenings on the floor of the buccal cavity. Near the posterior end of the buccal cavity is a pair of structures appearing tongue-like in transverse section, (Fig. 14, T) They rise from the lining epithelium, from a latero-ventral position, one on each side

of a median ventral longitudinal thickening (Fig. 14). These tongue-like structures project into the lumen of the buccal cavity at an angle of about 39-45 degrees with a frontal plane and their free margins are often closely approximated. These organs are evaginations of the lining epithelium and are structurally like it. They appear to be the structures mentioned by Beddard (195, p. 33), Michaelsen, and Ude ('92, p. 67) but the treatment in all cases is so scanty that it is difficult to determine exactly the nature of the organs to which they refer. Vejdovsky ('84, p. 99) discusses these organs briefly and gives figures of the same as they appear in *Anachaeta bohemica* Vejd. According to his figures, these "Geschmacksläppchen" resemble the organs in question in *F. firma* but there seems to be quite difference in the structure. However since no other modifications of this region is described, it seems probable that these are the same organs. Michaelsen once referred to them as serving the purpose of a sucker. Beddard states that they are probably sense organs and that they are provided with minute hair-like processes which which I have not been able to demonstrate in any of the species studied by me. Ude evidently regards them as taste organs originating from the epithelial lining but does not give his evidence for this conclusion.

A thin muscular layer, which is a continuation of the musculature of the body wall, bounds the basal part of the lining epithelium. Radiating from this muscle layer in the anterior part is a number of muscular strands which cross the body cavity and unite with the muscular layer of the body wall (Fig. 13, Mu). The thin peritoneal membrane forms the inner coat of this buccal cavity.

Pharynx.

The buccal cavity is followed by the pharynx which is characterized by a massive dorsal thickening of the epithelial lining of the tube throughout its entire length. The cuticula continues as an unmodified lining throughout this region but the epithelial and muscular layers are distinctly differentiated. At the beginning of the region the epithelial layer abruptly acquires dorsally, a thickness amounting to about six times the original thickness (Fig. 13, Ph). In the middle extends a deep longitudinal furrow. The cells of the epithelial thickening (Fig. 17) are long, tapering slightly towards the inner ends and appear glandular in structure. Michaelson claims to have seen tactile sensory organs between the cells but I have been unable to demonstrate the existence of such in *F. firma*.

The entire dorsal muscle layer gives rise to a conspicuous mass of muscular strands. Muscular strands also rise from the muscular layer of the body wall directly opposite. The muscles from the pharynx and those from the body wall meet along a line in a pinnate fashion as indicated in figure 13, Mu.

Oesophagus.

The posterior limit of the pharynx is marked by the abrupt resumption by the dorsal epithelial lining, of the typical form and thickness. At this point there begins a division of the tract which is commonly called the oesophagus. It is identical in structure with the buccal cavity except that the epithelial layer is slightly thickened. It is difficult to define the posterior limit of this region and to reconcile some conflicting anatomical and embryological views. The cuticular lining extends as far posteriorly as the origin of the peptonephridia while

beyond this point (anterior part of IV) the canal has no cuticular lining but is ciliated and is of uniform structure throughout the remainder of its length excluding the last seven somites. This fact suggests that the termination of the cuticula and its replacement by cilia marks the terminus of the oesophagus. But some authorities state that the spermathecae, which are attached to the alimentary canal in the posterior part of V, are of ectodermic origin in this group and furthermore Beddard('95,p.54) claims that the septal glands, located in IV,V, and VI,are of ectodermic origin, that they are simply hypodermic glands which have been invaginated along with the stomodaeum and that the part of the canal which they surround must be of hypodermic origin. This would put the beginning of the intestine much farther back than the openings of the peptonephridia. Since the embryology of these forms is still very incomplete, it does not seem possible to establish the limits of these regions on the basis of their development. There is a distinct and abrupt transition from the cuticular lining to the ciliated epithelium at the peptonephridial openings and I shall arbitrarily refer to the region between it and the pharynx as the oesophagus. Type sections of *F. agilis* Smith show a very interesting condition in which there is a surprising difference in the intensity of the staining in this region. All of the oesophagus takes the stain in a moderate degree but beginning at the posterior edge of the peptonephridial apertures, The intestine appears to have a strong affinity for the stain and the coloration is very intense. This fact aids in establishing this point as a place of division between two distinct regions.

Peptonephridia.

Appended to the ventral side of the posterior part of the oesophagus is a pair of structures, formerly known as salivary glands but now known as peptonephridia. This name was first used by Benham and since then it has been adopted by most of the well known writers on Oligochaetes. That they are intimately connected with the oesophagus is indicated by the fact that the cuticula lines their canals for a short distance (Fig. 18). Owing to differences in the various specimens in the state of contraction of the anterior part of the digestive tract, and also to the obscured condition of the anterior septe, it is a little difficult to determine the precise segmental position of these openings. After careful study, I place them in the anterior part of the fourth somite very near the septum III/IV (Fig. 13, Pn). An examination of the type sections of *F. agilis* Smith shows that a similar difficulty is encountered but in this species they appear to open in the posterior part of III very near the septum III/IV. At a short distance from the oesophagus these peptonephridia begin branching. They are directed posteriorly and lie ventral and parallel to the intestine. They extend through IV, V, and a short distance into VI, giving off branches irregularly along their whole length. Each branch has a central lumen which unites with those of other branches and communicates with the alimentary canal by one short main duct. The lumen of these organs seems to be intracellular.

The peptonephridia are often discussed under the head of nephridia since some authorities assert that they are of nephridial origin. Other investigators take a contrary view. The evidence advanced in either case seems about equally inconclusive. Those holding the former view base their claim chiefly upon the intracellular nature of the lumen, the

position in the body, and the absence of normal nephridia in the region of the body occupied by these organs. The other view is based on the absence of an opening into the coelom and of any trace of a funnel; the absence of cilia in the lumen; and the regular lack of nephridia in the anterior somites of the lower Oligochaetes. Because of the unsettled condition of the matter and owing to the intimate organic connection of these organs with the digestive tract, they are regarded in this paper as accessory organs of the alimentary system.

The arrangement and character of the muscles in the first three regions of the alimentary canal indicate that they are not so much concerned with the mere action of the tract itself as with a limited eversion and introversion of the anterior part. The varying backward positions of the anterior septa also indicate that the anterior regions constitute a small introvert.

Intestine.

The intestine is a nearly straight tube of uniform character which, with some diminution in size, extends to the terminal anus (Fig. 13, I). The differentiation into regions is very slight but the following divisions may be established: (1) the anterior, comprising V-XII; (2) middle or chylus cell region in XIII-1/3 XVIII; and (3) the posterior region which includes all somites posterior to XVIII.

Structurally the anterior region consists of an inner layer of ciliated epithelial cells, a middle muscular layer, and on the outside, for most of its length, a thick layer of chloragogenous cells.

Surrounding the anterior part of this region are the three pairs of septal glands (Fig. 13, St', St'', St'''). They are masses of glandular cells

attached to the anterior surfaces of septa IV/V, V/VI, and VI/VII. The right and left members of the first pair arch over the intestine and fuse at the point of contact. The members of the second and third pairs also arch over the intestine and closely approach each other but do not unite. The members of each of the three pairs are discontinuous on the mid ventral side. These glandular masses are composed of large nucluated pear-shaped cells each of which is prolonged into a narrowed part which serves as a duct. The ducts of each member of the third pair converge ventrally to form two tissue columns which extend anteriorly, one on each side of the median line and ventral to the digestive tract (Fig. 16). These columns receive the duct columns of the second and first pairs respectively and then, taking an upward diagonal course, they attain a position dorsal to the oesophagus just posterior to the pharynx. Both columns give off three branches, an anterior, a median, and a posterior, which unite with the corresponding parts of the pharynx. Evidently the products of the septal glands are poured into the pharynx and function in the early stages of digestion and are in no way connected with the intestinal digestion.

Immediately anterior to the second pair of septal glands on the dorsal surface of the digestive tract are the intestinal connections of the two spermathecae (Fig. 13 and 15, IQ).

The middle or chylus cell region, as previously described, includes somites XIII-XVIII (1/3 of latter)- This region is characterized by the presence of peculiarly differentiated cells known as chylus cells and which are here very numerous. The intestine in this region is lined by a layer of somewhat rectangular, ciliated epithelial cells which are

approximately regular in outline and each contains a large spherical nucleus. The chylus cells lie deeper in the intestinal wall and open through this epithelial layer into the lumen of the intestine. They are long, rather narrow, and broader at the base than at the apex(Fig. 19,Chy, Fig. 20). They are unique in possessing a canal which opens into the intestinal lumen at the apex and extends to the base of the cell. The apical part of the canal is straight but elsewhere it tends to become somewhat tortuous, especially in the broad basal part. The canal ends blindly at one side of the base. The elliptical nucleus lies in the base of the cell in an angle of the canal(Fig. 19,N). The cell walls are indistinct and it is somewhat difficult to determine the exact line of demarcation between adjacent cells. However, sufficient details of structure can be made out to prove that these cells are definite unit structures and that the canal of each cell is confined entirely within the limits of that cell. There appears to be a certain amount of variation in the shape of these cells. In regions near septa and sometimes at the sides of the intestine, they are rather short(Fig. 19) while in regions midway between septa they may be rather long and slender(Fig. 20). However, in all cases the general structure and arrangement of parts is constant. These cells form a continuous layer. Interstitial cells are evidently not present and the epithelial cells do not seem to project between the chylus cells. The intracellular canal is surrounded by a definite layer of cytoplasm of uniform thickness which differs from the rest of the cytoplasm in being more hyaline and in staining less intensely. The junction between these two kinds of cytoplasm appears, in stained sections, as a definite dark line. The remaining cytoplasm of the cell is finely granular and stains profusely. The apical part of the canal is characterized by the

presence of cilia which rise from the lining. The basal part of the canal is entirely devoid of cilia. The bases of the chylus cells are in direct contact with blood sinuses(Fig. 19,B.S.).

Such cells were first discovered by Michaelson(in *Enchytraeus hegemon* and *E. tenuis*; in part old names) who worked up their structure in some detail and made an attempt to establish their homologies and functions. Eisen('04) made careful studies of such cells in the species which he described and demonstrated to his own satisfaction that the location, form and size of these cells present good specific characters. For some reason Eisen failed to give the measurements of these cells in his various species and does not indicate the magnification of his drawings, hence little can be determined concerning his third criterion. Since the other investigators have not described such structures, Eisen's conclusions were derived from the examination of only a small number of the known species of the genus. Studies must be made of the other species before his views can be fully established; otherwise they remain open to question. A study of the two species described in this paper confirms the conclusion of Eisen. In comparison with the other species in which these structures have been studied(see p.83) *F. firma* is characteristic in having the chylus cells in XIII-1/3XVIII and in having a continuous layer of them bounded internally by block-shaped epithelial cells(Fig. 19,Eth).

An examination of the type sections of *F. agilis* Sm. shows the presence of chylus cells in XIII-XVI. They are somewhat long and slender and possess the characteristic intracellular canal which is ciliated only in the apical part and is branched in the basal part. In sections, the ciliated lining epithelial cells of the intestine appear deltoid in form.

They are wedged in between the apices of the chylus cells thus exposing only one surface to the lumen of the intestine. No interstitial cells are present. The condition existing in this species also confirms Eisen's conclusions.

The homologies and functions of these peculiar cells are quite problematical. Their intimate connection with the digestive tract and their close contact with the blood system indicate that they have an important role in some metabolic process. Michaelson maintains that they are organs of absorption and not of secretion. Eisen also favors this interpretation and explains it by supposing that the presence of the cilia in the canal indicates that the canal itself is simply an invagination of the ciliated surface of the cell and that a means is thus provided for the bringing of the nutritive fluid into close contact with the blood sinuses at the base of the cell. Eisen further holds that the probable function of the cilia in the apical end of the canal is to facilitate the introduction of the nutritive fluid into the canal and that the canal is the means whereby greater intestinal surface and rapid absorption is insured without any diminution or weakening of the intestinal wall. Professor Smith has called the attention of the writer to a paper by Cuénot('97) which, although not dealing directly with this subject, throws light on the problem in an interesting way. Cuénot has shown that the vibratile cilia in the nephrostome of the nephridia of Oligochaetes cannot introduce the coelomic fluid into the interior of the nephridia except when the lumen is empty. Furthermore he has shown that solid bodies in suspension in the coelomic fluid cannot pass through the orifice of the nephrostome because the thickly set cilia of the nephrostome plays the role of a sieve or filter and is an impassible barrier to solid particles.

Therefore it seems that the prime function of the cilia of the nephrostome is to prevent the passage of solid particles into the nephridial lumen and not to introduce fluids into the lumen as has sometimes been supposed.

It seems highly probable that the cilia in the apical part of the chylus cell canals have a similar function and that they do not facilitate the introduction of the nutritive fluids into the canal as Eisen thought. No experimental evidence has yet been secured to substantiate this view but it seems very plausible. In fact, with Cuénot's work as a basis, it seems that there are more reasons why this should be the case in the chylus cells than in the nephridia. In the first place, the canals of the chylus cells end blindly while the nephridial canals have external openings and in consequence the nephridial lumen may sometimes be almost or entirely empty and then, as shown by Cuénot, it is possible for the cilia of the nephrostome to aid in introducing the coelomic fluid. On the other hand, the chylus cell canals, occurring in a region of the intestine where, normally, the nutritive fluid is constantly present, and having but one opening, they presumably are constantly filled with fluid so that it would be impossible for the cilia to introduce the fluid. In the second place, the chylus cells are exposed to a greater quantity of solid matter since all of the contents of the digestive tract pass by their open ends. None of the preparations examined by the writer showed any indication of the presence of solid matter in the chylus cell canals such as was present in the intestinal region near them. Unless some provision was made against the possibility of the entrance of solid matter, these blind canals would be liable to be filled with solid matters and their functional efficiency be markedly reduced.

Michaelson and Eisen both claim an adaptation to the absorption

function based on their observations that most of the cells have their apices inclined towards the anterior region of the worm and they interpret this as facilitating the absorption of the nutritive fluid. This condition is not very apparent in preparations of *F. firma* since many of the apices of the cells are inclined toward the posterior region and some meet the lumen at right angles. However, it is the belief of the writer that the inclination of these cells is, to some extent, dependent on the state of contraction of the intestinal tract and the body wall. Eisen also sees digestive and protective adaptations in the presence and character of the lining cytoplasmic layer of the canal.

The posterior region of the intestine includes all of the somites posterior to XVIII. This part of the intestine is a straight tube in which the diameter diminishes slightly toward the anus. In structure it resembles the anterior intestinal region but has in addition the blood sinus region between the muscular layer and the lining epithelium(Fig.21). The only noteworthy differentiation is the posterior part which is lined with a reflection of the external cuticula for a distance of about seven somites. The epithelial layer in this region is thrown into five or six strong longitudinal folds which appear conical in transverse section(Fig. 21,Eth). In the last three somites the muscular wall of the intestine is joined to the muscular layer of the body wall by several strong muscular strands which evidently control, to some extent, the position of that particular part of the canal.

Blood Vascular System.

This system presents the same simplicity as that which characterizes the other members of this group. The main trunks are as follows:- The

dorsal vessel rises from the intestine in a postclitellar position and extends anteriorly along the mid dorsal line of the alimentary canal to a position just ventrad to the brain where the vessel divides into two trunks which diverge, each forming a loop on its respective side of the alimentary canal from which it extends in a posterior direction. These two trunks finally approach each other on the ventral side of the intestine and fuse in the region of the first pair of septal glands to form the ventral trunk which extends to the posterior end of the body. No attempt has been made to work out the finer vessels. The numerous perivisceral blood sinuses in the intestine make obvious the intimate relation which the blood has with the nutrient fluids.

Excretory System.

This system presents no striking departure from the conditions described for the other closely allied species. Paired nephridia are present in all somites of the body except the first five, the clitellar, and the anal. The first pair is developed on VI/VII. The anteseptal part approximately equals the postseptal part (Fig. 35). The duct rises from the postseptal part a short distance back of the septum and opens out through the body wall just in front of the ventral setae. The lumen follows a more or less contorted course in both anteseptal and postseptal parts.

Nervous System.

This system consists essentially of three parts; viz., (1) brain; (2) circumoesophageal commissure; and (3) the ventral nerve cord. All parts are closely invested by a well developed neurilemma.

The brain occupies a median dorsal position in the anterior part of II and may project slightly into I (Fig. 13, Br). The length is one and

one fourth times greater than the width; the sides are nearly parallel; the anterior part is concave and the posterior part is convex(Fig.36).

The anterior part of the brain gives rise to two trunks which diverge, each forming an anteriorly directed loop from which they extend around the digestive tract and meet below in II to form the suboesophageal ganglion which represents the beginning of the ventral nerve cord. Shortly after their origin from the brain each of these trunks gives off a branch which extends cephalad to innervate the prostomium. This circumoesophageal commissure is composed exclusively of nerve fibers.

The ventral nerve cord(Fig. 37) is a chain of nerve elements extending from II to the posterior end of the body. It lies on the mid ventral line immediately above the muscular layer of the body wall. A sheath of tissue binds it ventrally to the body wall. A series of enlargements and constrictions mark off the so called ganglia and correspond to the metamerism. Thus far I have been unable to demonstrate any lateral nerves arising from it. The major part of the mass of the cord is composed of fibers while the cells are localized on the ventral side.

Reproductive System.

The position of the chief organs of this system conforms to the regular Enchytraeid plan. The clitellum is on XII-XIII; the spermathecae in V; the spermaries in XI; the ovaries in XII; the spermiducal pores on XII; and the oviducal pores on XIII.

Spermaries.

The spermaries are developed from the peritoneum of the posterior side of septum X/XI (Fig. 38,T). They are more or less lobed and are made up of spherical cells(primitive sperm cells) many of which appear in

the different stages of mitosis. Dorsal to the spermaries lies a mass of developing sperm which has separated from the spermaries and is undergoing the later stages of development in the body cavity(Fig. 38,Spm). In preparations of sexually mature specimens this mass is quite extensive, filling most of the body cavity in that region and often pushing the septum X/XI almost in contact with septum IX/X, and the septum XI/XII almost in contact with septum XII/XIII. The developing sperm cells are mingled with the very long cilia which extends from the opening of the spermiducal funnel into the body cavity.

Sperm ducts and funnels.

A pair of well developed sperm ducts is present. Each consists of three distinct parts;viz., the funnel, the duct, and the penial bulb (Fig.38,F,D,Pl). The funnel(Fig.29) is barrel shaped and the length is approximately one and a half times greater than the diameter. The funnel is situated in the posterior part of XI with its base in close proximity with the lower part of septum XI/XI and the long axis of the organ is directed obliquely dorsad. The anterior end is characterized by a well differentiated, reflected collar, distinctly set off from the body of the funnel by a circular constriction. This collar surrounds the mouth of the funnel and through it emerges the extremely elongated cilia. The bulk of the funnel is composed of glandular cells of extraordinary length(Fig.31) which encroach on the lumen and reduce it to an extremely fine canal. The nuclei lie in the peripheral ends of the cells. The side of the funnel nearest the median line shows a groove like structure which runs the length of the funnel and which in section appears as a thinning of the funnel wall. The periphery is covered with a thin layer of peritoneum.

The duct rises from the posterior part of the funnel, passes through the septum XI/XII into XII and there becomes much contorted. From this confused mass it extends to the penial bulb and unites with it (Fig. 38). A transverse section of the sperm duct shows an external, thick, epithelial covering beneath which lies the lining epithelium which is composed of a single layer of conspicuously nucleated cells. The lumen is very fine and seems to be ciliated.

Penial bulb.

The penial bulb or copulatory cushion is an oval structure composed of muscular and glandular tissues situated at the posterior end of the sperm duct. The organ was seen and described by a number of the early investigators (Michaelsen, Vejdovsky, et al.) but the finer details of structure were neglected and no attempt was made to discover taxonomic characters in the structure of the organ. Eisen ('04) made critical studies of the organ in fifty one species, nine of which belonged to the genus *Fridericia*. After acknowledging the fact that no data is available from earlier investigations, the results of this study are stated by Eisen as follows:- "It seems almost certain that a great uniformity of structure exists in the different species of the same genus or in the same genera of the various subfamilies. The structure of the penial bulb or corresponding organs can therefore be said to be highly characteristic of both species, genera, and subfamilies!" According to his observations in the *Enchytraeidae*, there exists three distinct kinds of bulbs which he defines as follows:-

"I. The Mesenchytraeid Bulb.

A single muscular structure containing circular as well as fan shaped muscle bands connecting the body wall with the periphery of the

bulb. Between the muscular bands are generally found penial glands which open on the surface of the bulb around the penial pore. The sperm duct penetrates the bulb, opening on the center of its outer surface.'

'II. The Enchytraeid Bulb.

A multiple bulb consisting of several separate cushions grouped around the penial pore. In these cushions are found several sets of fascicles of glands, each fascicle opening by itself on the surface of the body. No muscular bands connecting the base of the cushion with the periphery. Sperm duct never penetrating the bulbs or cushions but open close to and independently of them. Exterior to the cushions are numerous muscles connecting the body wall immediately surrounding the pore with other parts of the same somite.'

'III. The Lumbricillid Bulb.

Always single and covered with a strong muscular layer which however never penetrates down between the cells of the bulb. There are generally two or three distinct sets of glandular cells in the bulb. Some open in the lower part of the sperm duct or rather in a narrow groove in the elongation of the sperm duct. Others open on the free surface of the bulb either irregularly or in narrow circular fields bunched into fascicles. The sperm duct penetrates one side of the bulb.'

The eight genera examined by Eisen are distributed by him as follows:

I. Mesenchytraeid Bulb	{ Mesenchytraeus.
II. Enchytraeid Bulb	{ Enchytraeus. { Michaelsona.
III. Lumbricillid Bulb	{ Lumbricillus. { Marionina. { Eryodrilus. { Henlea. { Fridericia.

The penial bulb in *F. firma* has been studied with considerable care with the purpose not only of determining the structural detail but also of determining whether or not it bears out the conclusions of Eisen.

The description of this organ is attended with some difficulties because of the nature of the organ and also because of the fact that no nomenclature has yet been established for it. Therefore it will be necessary to make frequent references to the figures. Both organs of the pair are identical in structure and a description one will serve for both.

This organ lies in the ventral part of XII(Fig.27,Pl). At x,figure 34, there is a deep flattened invagination of the body wall which,however, includes only a part of the body wall; viz., the cuticula and the hypodermis. The muscular layers are interrupted at that region. Near the region of invagination(x), the hypodermis of the clitellum abruptly changes to a very different form(Fig. 34,T) in which there is a marked change in the shape and size of the nuclei and in the character of the cytoplasm. The cuticula, with a slight diminution in thickness, continues into the invagination as a lining. On the inner side of the invagination the hypodermal cells merge into a layer of cells which is clearly different from the former which open out upon a surface which Eisen seems to designate as the "'outer free surface of the bulb'"(U). The sperm duct(D) enters the outer side of the bulb and connects with the central chamber. This chamber curves laterally and opens at the penial pore(Po) at the base of the invagination. The body of the bulb is composed of two kinds of cells;viz., large, glandular, oblong cells(Gl) which occupy all of the upper and peripheral parts of the bulb and which are characterized by large, approximately spherical nuclei; and long, narrow, columnar cells (IB) which are arranged radially around the central chamber. They begin

at the junction of the sperm duct and the central chamber and form the boundary of the latter for its entire length. This last kind of cells stain lightly. Each cell contains a nucleus in the end which is distal to the central chamber and the constancy of this position of the nucleus accounts for the distinct row of nuclei which show distinctly in sections. Figure 28 shows them as they appear in transverse section of the central chamber. These latter cells merge gradually into hypodermal cells similar to those at (T). These, in turn, give place to the olitellar cells(Ep) which are present in the mid ventral region. The whole bulb is covered by a well developed muscular layer(PM) which is a continuation of the circular muscle layer of the body wall. Figures 27 and 34 show the details of this musculature. It will be noted that no muscular strands penetrate the bulb. Therefore this bulb is of the Lumbricillid type.

I quote the following from Eisen's characterization of the penial bulb of the genus *Fridericia*: "'There is only one kind of cells filling the bulb. These cells all open into the extension of the sperm duct and along the surface of the bulb.'" Eisen's figures agree with the above statement. His descriptions and drawings all show that cells of one kind only fill the entire bulb and it is the prolongations of these cells which meet the central chamber. Now it is evident that there are two distinct kinds of cells in the bulb of *F. firma*(Fig. 27,28,34). It must be acknowledged that the cell boundaries between the cells(GC) and (IB) are very difficult to identify but it is easy to demonstrate a nucleus at the distal part of each of these inner cells(IB) and these nuclei are rather constant in size and shape, being elliptical and very much smaller than those of the peripheral cells(GC). These facts are indicated in figure 28 which shows a transverse section of the central chamber(frontal

section of the worm).

An examination of the type sections of *F. agilis* Sm. reveals the fact that the penial bulb of that species agrees with that of *F. firma* in showing the presence of the same two kinds of cells. Also an examination of cotype material of *F. agricola* Moore shows the same plan of structure. Assuming that Eisen's descriptions and drawings are correct for his species, it appears that his generic character breaks down at this point. This matter will be discussed again in connection with the other new species which is described in this paper (page 48).

Spermathecae.

As is the rule in this family, with one exception, there is but one pair of spermathecae. They lie in V and dorsal to the intestine (Fig. 13, S). They lie obliquely in the coelomic cavity, the long axis pointing in a ventro-posterior direction. The lower ends converge towards the dorsal aspect of the intestine and extend under the second pair of septal glands and unite with the intestine. Each consists essentially of three parts; viz., (1) an ampulla; (2) diverticula; and (3) the duct.

The ampulla is a pear-shaped organ composing the bulk of the spermatheca (Fig. 22). The smaller end is united to the intestine; the upper enlarged portion bears the diverticula. The cavity within conforms somewhat to the external shape of the organ, being rather spacious in the region of the diverticula and gradually narrowing to the point where it communicates with the lumen of the intestine. The connections of the two spermathecae with the intestine are separate (Fig. 15). The upper enlarged end of the ampulla (Fig. 22) bears three to four lobe-like diverticula which are sessile and occupy about two thirds of the periphery, the origin

of the duct occupying the remainder. These diverticula are of two sizes, two large and one small, or when there are four, two larger and two smaller.

The duct, as before stated, originates at one side of the upper part of the ampulla from a cone shaped expansion embedded in the wall (Fig. 22). This expansion immediately diminishes in diameter to form the duct proper, which is constant in diameter, about three times as long as the ampulla, and opens to the exterior in a lateral position in the the region of the septum IV/V. No glands are present at its external opening (Fig. 9). It is lined throughout its entire length by the cuticula which seems to indicate its ectodermic origin.

Ovaries.

The ovaries are developed from the basal posterior surface of septum XI/XII (Fig. 38, O). They present no regularity of form. They show structurally a complete series of developing ova from the base where the primitive germ cells are least developed, to the free extremities where the cell masses are ready to separate from the organ. In preparations of this species one zone (Fig. 33, Z) seems to be especially mitotic. A number of masses of ova cells are present floating around free in the coelom (Fig. 27, EM). This appears to be the normal method of development of the ova. A number of partly mature ova cells break away from the free extremity of the ovary but still remain aggregated for some time. Some of the masses are composed of cells of about equal size; others are composed of cells of different sizes, frequently with one very large cell and the others of varying smaller sizes. In the former case, the mass is evidently of recent origin from the ovary and the constituent cells have not had sufficient time to develop to any considerable degree; in the latter case

the mass has been free for some time and the largest cell represents the nearly mature ovum about ready to separate from the mass and pass out as an ovum ready for fertilization.

Oviducts.

These structures seem to be degenerate (Fig. 26, Ov). They consist of little more than a pair of mere pores through the body wall on the ventral surface of XIII just posterior to the septum XII/XIII. Viewed externally, the apertures are circular in outline. Sections show the diameter of the channel to be approximately constant as it passes through the cuticula and the hypodermis, but rapidly diminishes from thence until it attains its minimum in the longitudinal muscle layer. There it immediately increases in diameter and forms a funnel shaped structure extending into the coelom and directly somewhat anteriorly toward the adjacent septum XII/XIII which seems to be reflected toward the posterior region at a corresponding position to meet this inner expansion of the oviduct.

The cuticula is merely perforated at the external opening and is not reflected inward as a lining. The hypodermal cells which form the walls of the pore are slightly different from the adjacent clitellar cells (Fig. 26). In comparison with the latter they are about the same length but are narrower and more crowded; the elliptical nuclei are larger, more regular in outline, and each is located near the center of its respective cell; the cytoplasm has a greater affinity for the stains. The inner funnel shaped region is composed of heavily nucleated, irregular, thin cells in which the cell walls are obscured. The indefiniteness of the form and size of the organ and the size, shape, arrangement and structure of the cells of the inner funnel is very suggestive of degeneration.

A striking contrast is offered in the small size of the oviducts and the very large size of the eggs which are conveyed by them. Early investigators(d'Udekem, et.al.) overlooked these small pores and advanced the theory that sperm ducts conveyed both sperm cells and ova. Buchholz opposed this opinion and since it was known that the ova easily change their shape, advanced the theory that there might be small openings through the body wall through which the eggs escaped. Claparède first described these pores and Vejdvosky verified the observation by treating the worms with osmic acid which caused the pores to open widely and occasionally eggs were seen to pass out. It is evident that the passage of the eggs is permitted by the capability of the pores to undergo limited distension and the ease with which the eggs can change their form.

A large part of the coelomic cavity in XII is filled with a peculiar granular, noncellular substance(Fig. 26,27,38,Y) concerning the nature of which the writer is in doubt. Structurally it seems to be only a homogeneous mass of some granular substance which stains with eosin to a marked degree but does not stain with haematoxylin at all and appears distinctly different from any other material of the organism. A similar substance appears in sections of *F. agilis* Sm. in the same position. Stephenson found something like it in *F. stewarti* Steph. and called it yolk substance but did not give his reasons for the name.

DESCRIPTION OF FRIDERICIA TENERA NOV. SP.

Definition.

Length 9-17 mm.; average 12 mm. Somites 52-59; average 55. Color whitish. Prostomium rounded. Dorsal pores begin on VII. Setae of unequal length, the inner ones being shorter; usually six in the ventral bundles and four to five in the lateral bundles in the anterior part of the body; usually but two per bundle in the posterior region. Head pore O/I. Clitellum on XII and XIII. Septal glands in IV, V, and VI. Peptonephridia branching, the branches originating from a common base. Brain about one and one half times longer than wide; the posterior margin is convex, the anterior margin is concave; sides converge towards the anterior. Dorsal vessel rises posterior to the clitellum. Spermathecae with barrel-shaped ampullae connecting with the intestine in V and each bearing about seven globular, sessile diverticula at its upper extremity. Anteseptal and postseptal parts of the nephridia about equal in size; the efferent duct rises from the anterior region of the postseptal part near the septum. Spermiducal funnel about twice as long as wide; its duct is long, much contorted and confined to XII. Lymphocytes elliptical.

As in the preceding species, the specific value of the penial bulb and the chylus cells will be discussed later (page 45).

Found in a compost pile in the Forestry Grounds of the University of Illinois. The specimens were collected in October and November and all were found to be sexually mature.

Affinities of *Fridericia tenera* nov. sp.

This species seems to be rather closely related to several other

species. The character of the spermathecae puts it in the group of species having many diverticula. The other specific characters indicated below relate it to *F. lobifera* Vejd., *F. udei* Br., *F. macgregori* Eisen, *F. californica* Eisen, and *F. beddardi* Br. The descriptions of *F. udei* and *F. beddardi*, because of brevity, use of relative terms, and indefinite statements, are somewhat puzzling and make comparisons difficult. However the aggregate of differences is such it is not difficult to separate this species.

The following table will indicate the similarities and differences of the above species.

F. taberna nov. sp.

F. lobifera Vajda.

F. udei Br.

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F. beddardi Br.

F. macgregori Eisen.

F. californica Eisen.

	<i>F. taberna nov. sp.</i>	<i>F. lobifera</i> Vajda.	<i>F. udei</i> Br.	<i>F. beddardi</i> Br.	<i>F. macgregori</i> Eisen.	<i>F. californica</i> Eisen.
Length	8-17 μ .	15-20 μ .	10-20 μ .	10 μ .	6 μ .	22 μ .
Abdomen	52-59	55-60	60.	About 55.	about 45.	70.
Saliv	In anterior region mostly 6 in ventral bundles and 4-6 in lateral bundles. In posterior region mostly 2 in a bundle.		4-6 in a bundle.	4-6 in a bundle.	6-8 in the ventral bundles 4-6 in the lateral "	
Peptonephridia		Secondary branches Branched & usually secondary branches	Large and ramifying.			
Brain				Little longer than wide. Side margins converging to vent front. Ant. slightly con- vergent. straight. Ant. branches diverge widely.		Anteriorly and posteriorly x 1-2 times longer than wide.
Spermathecae				With 10 sessile diverticulae. Duct twice as long as apophysis. Two oval cells located at the external opening.		Row of 4-7 bladder-like diverticulae.
Nephridia	Antesepal and postsepal regions about equal. Duct rises from the anterior part of the latter.		Antesepal region 1/2 as large as the postsepal. Duct rises near the septum.	Large antesepal region and somewhat larger postsepal from which the duct rises close to the septum.	Antesepal and postsepal regions about equal in size. Duct rises from the anterior part of the latter.	
Funnel		Not described.	Not described.	Length, the diameter. Collar broad, small, but distinctly set off.	Not described.	
Cyphocyte	Elliptical	Not described.	Round to oval.	Round to oval, thick irregular nucleus.	Large, oval.	

In connection with the above comparison a certain discrepancy which appears in Eisen's description of *F. macgregori* should be noted. In the description of this species the following statement is made concerning the brain: "'Brain anteriorly much convex; posteriorly slightly so!'" A text figure of the brain is given and shows exactly the opposite condition. The posterior part is much convex while the anterior is only slightly so. The writer has accepted the figure as representing the correct condition since there seems to be smaller chance of error in a drawing than in a description.

A complete detailed description of this species would be largely a repetition of the description given for *F. firma*; hence only those characters which especially differentiate the species will be discussed.

External Characters.

In general appearance, shape, segmentation, body regions, and external apertures this species resembles the preceding one. However, distinct differences in size, color, clitellum, and setae are presented.

F. tenera is much smaller than *F. firma*. The length of the former is variable. Measurements of sixteen specimens taken at random showed the extremes to be 9 and 17 millimeters with an average of about 12 millimeters. The body is almost circular in transverse section. The diameter is a maximum in the region of the clitellum where it is about 0.4 mm. The number of somites in fifteen specimens ranged from 52 to 59, with an average of about 55.

The color is more whitish than is that of *F. firma*, lacking the distinct yellowish tint of the latter. The glistening appearance is also absent. All specimens are opaque. The clitellum is indistinct and

includes XII and XIII.

The setae of this species resemble those of *F. firma* in number and arrangement but in size they are much smaller and the proximal end is more recurved and the termination is more acute. The relative size of the various setae in a bundle conforms to the description given for *F. firma*, indicating the single instead of the paired origin. The ventral setae bundles usually contain six setae in the anterior region, four in the middle region, and two in the posterior region. The lateral bundles contain four or five in the anterior region and two in the posterior region.

Internal Anatomy and Histology.

Body Wall.

The body wall is made up of the usual four layers. Aside from the proportionate diminutions in the thickness, the cuticula and its relation to the surface and various apertures of the body, conforms to the condition described for *F. firma*. The hypodermis presents a marked difference in the presence of numerous unicellular goblet-like gland cells. These gland cells are imbedded among the ordinary hypodermal cells and open through the cuticula by means of the distal, narrowed neck region (Fig. 42). They are much larger than the hypodermal cells but do not equal them in length, thus being almost entirely surrounded by hypodermal cells. These gland cells are present all over the body and are approximately constant in shape except in the thickened region of the first somite and the prostomium where the gland cells are proportionately elongated. The contents exhibit a certain degree of polarity. In the distal part of the cell the contents are of such a nature as to take the stain only to a slight degree. The proximal part is filled with

a seemingly different substance which takes the stain more intensely and in which a conspicuous nucleus is imbedded. The cytoplasm, to some extent, has a fibrillar appearance.

The clitellum is markedly distinct from that of *F. firma*. Structurally it is made up of granular cells, nucleated at the base and arranged in transverse rows but alternating with clear, non granular cells (Fig. 41).

The muscular layers are structurally like those in *F. firma* except for a difference in the form of the individual units of the tube muscles. Instead of the somewhat rectangular shape which they show in transverse section in *F. firma*, they are elongated, flattened and the granular lumen is slit like in appearance.

The peritoneum has the usual structure. The cells of the chloragog layer are finely granular, nucleated, and somewhat elongated radially with reference to the intestine.

Coelom.

The coelom presents no special differences from the typical condition. It communicates, as usual, with the exterior by means of the spermiducal pores, oviducal pores, nephridial pores, head, and dorsal pores. Most of the somites are filled with elliptical lymphocytes.

The Digestive System.

The peptonephridia open into the digestive tract at the junction of the oesophagus and the intestine in IV. These organs are composed of numerous branches rising from a common base. Most of these branches are directed posteriorly and terminate in VI.

The chylus cell region includes that part of the intestine lying in XV-XVII. The chylus cells are flask shaped and contain the characteristic

canal which is somewhat sinuous in outline, particularly in the basal region of the cell(Fig. 43). The well developed nuclei lie as usual in the angle made by the canal. The canal is ciliated for almost the whole length. A cytoplasmic lining layer of the canals seems to be absent in these cells. Spacious blood sinuses surround the basal parts(BC). Between the apical ends are fitted the wedge shaped ciliated epithelial cells which constitute the greater part of the inner lining surface of the intestine. The position and structure of the chylus cells appear to be distinct from that of any other species in which they have been described(see table, p.50), and as far as our knowledge extends, seem to offer specific characters.

Reproductive System.

The major part of the description of this system given for the preceding species holds good for this species and renders repetition unnecessary. However, the spermathecae, spermiducal funnels, and penial bulbs present distinct differences and require detailed description.

The spermathecae lie in V, joining the intestine on the dorsal side. Instead of projecting diagonally cephalad, laterad, and dorsad as in the preceding species, they project diagonally cephalad and laterad. The three chief regions, ampulla, diverticula, and duct, are clearly differentiated(Fig.46). The ampulla is comparatively elongated and is somewhat inflated at the middle region. At the distal end it bears a circle of sessile, globular diverticula, usually seven in number and not perfectly uniform in shape and size. However, the range of this variation is rather small. The duct springs from the center of this ring of diverticula and extends with few curves to its external opening in a lateral and very anterior position in V. Two pear shaped glands are

present and closely associated with this external opening(Fig. 46, Sd.G). As in the preceding species, the external cuticula is reflected inwards to form the lining of the duct for its entire length. Longitudinal sections of the ampulla show this organ to be partially filled with a substance which stains deeply and which appears to be composed of fibers or cilia. These structures lie parallel to each other and to the walls of the ampulla and extend through the ampullo-intestinal opening into the digestive tract . The writer is in doubt as to the nature and origin of this substance. Careful examination has failed to show any organic connection between the walls of the ampulla and this mass of material.

The spermiducal funnel is about twice as long as the length of the diameter and the posterior part is bent in a ventral direction(Fig. 45). The collar is clearly marked off by a constriction and is somewhat reflected. Histologically, this funnel agrees with that of the preceding species.

While the penial bulb is similar in position and musculature to that of the preceding species, in other structural respects it is quite distinct. Unlike that of *F. firma*, the body of the bulb is composed of cells of only one type(Fig. 49, GC). These are large, granular, conspicuously nucleated and have their long axes directed, in general, toward the outer surface of the bulb and many have greatly elongated processes (Pro) which lie parallel to each other and end radially around the lumen of the central chamber. These long processes thus take the place of the inner second type of cells found in *F. agilis*, *F. agricola*, and *F. firma* (Fig. 34, IB) and thus agree with Eisen's general conclusion that there is only one kind of cell in the bulb. The body invagination and the central chamber are lined by an inward reflection of the cuticula. The

sperm duct does not enter the bulb dorsally as in the three above mentioned species but enters the anterior end and extends diagonally ventrad to meet the central chamber. Figure 49 shows the structural detail of this organ as it appears in a transverse section of the worm. Figure 50 shows it in its protruded condition as it appears in a longitudinal section of the worm. This bulb is clearly of the Lumbricillid type. It is evident from Eisen's figures and descriptions that by coincidence he must have had only species having this particular type of bulb when he made his generic generalization and had not seen species of the type represented by *F. agilis*, *F. agricola*, and *F. firma*. It is true that in connection with his figure of the penial bulb of *F. harrimani*, he describes it as having two kinds of cells, one of which open into the lower part of the sperm duct, the other on the "outer free surface of the bulb" but by the former he refers to the body gland cells of the bulb and by the latter he means those cells lying above the central chamber and opening on the invaginated surface and does not refer to those inner central chamber cells present in *F. agilis*, *F. agricola*, and *F. firma*.

Excretory System.

Paired nephridia are found in all somites except the first five, the clitellar, and the anal. The first pair is developed on VI/VII and the anteseptal and postseptal parts are about equal in size. Figure 47 represents the characteristic shape and proportions of this organ. The nephrostome is ciliated. The efferent canal rises from the anterior part of the postseptal region and opens through the body wall to the exterior in front of the ventral setae. The lumen follows a very irregular course in both regions and is rather tortuous throughout the length of the efferent duct.

Nervous System.

The brain lies entirely in II. The length is about one fifth longer than the width. The anterior margin is concave and the posterior margin is convex. The sides converge very gradually toward the anterior. Two nerve trunks rise from the anterior and extend anteriorly, almost parallel, for about one third the length of a somite, then diverge and extend around the buccal cavity forming the circumoesophageal commissure. The very slight divergence of the commissural roots is distinctive of this species. Each branch gives off, from a point near the dorsal divergence, a branch which extends anteriorly to innervate the prostomium. The other parts of the nervous system have no special peculiarities and call for no discussion here.

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COMPARATIVE STUDY OF CHYLUS CELLS.

Species	Position	Shape	Shape of apical lining	Capal lining	Cells	Succosa	Endothelial cells	Interstitial cells
<i>P. terrestris</i> Eisen.	IX-XIII	Base truncate; sides converging towards apical end.	Apical part straight; basal part bent at right angles to apical part. Base thus formed will point towards base.	Distinct membrane	Along apical part.	In contact with base only.	Long and trumpet shaped; about two between each chylus cell and its neighbor.	Present; spindle shaped; one or two between the chylus cells.
<i>P. johnsoni</i> Eisen.	X-XII	Long and narrow; with somewhat early surface.	Almost straight for entire length.	Specialized layer of cytoplasm.	Along almost entire length.	In contact with base only.	Long and trumpet shaped; occur singly between the chylus cells.	Absent.
<i>P. cashi</i> Eisen.	XIV-XVI	Long and narrow; about twice as wide at base as at apex.	Apical part straight; digitate at base.	Specialized layer of cytoplasm.	Along apical 2/3 of length.	In contact with base only.	Rectangular; occur singly between the chylus cells.	Large; wedge shaped; two between chylus cells.
<i>P. mormon</i> Eisen.	XIV-XVI	Very broad and short.	Sigmoid and much twisted.	Specialized layer of cytoplasm.	Along apical 1/3 only.	Around base and sides.	Small and rectangular; three between chylus cells.	Absent.
<i>P. santarosae</i> Eisen.	XIV-XVI	Somewhat pear shaped; length about 3 1/2 times greatest width.	Apical part straight; branched at base.	Thick specialized layer of cytoplasm.	Apical 1/6 only.	Around base and part of sides.	Irregular; 3-4 between chylus cells.	Absent.
<i>P. vanregeneri</i> Eisen.	XIV-XVI	Long and narrow; base slightly expanded.	Apical part straight; basal part twisted.	Thick specialized layer of cytoplasm.	Apical 2/3 only.	Around base only.	Long; trumpet shaped; occur singly.	Absent.
<i>P. californica</i> Eisen.	XIV-XVI	Long and stout of equal width throughout entire length.	Straight for major part of course with short spur in base which is bent about 90°.	Thin specialized layer of cytoplasm.	Apical 3/4 only.	Around base only.	Long and expanded; lower end attenuated; 1-2 between chylus cells.	Absent.
<i>P. agilis</i> With.	XVII-XVI	Long; gradually expanding toward base; length 3-4 times width.	Apical part straight; branched at the base.	Specialized layer of cytoplasm.			Wedge shaped; seem to occur singly.	Absent.
<i>P. firma</i> nov. sp.	XVII-1/3 XVIII	Long; gradually expanding toward base; length 3-4 times width.	Apical part straight; sigmoid at base.	Thick specialized cytoplasmic layer.	Apical 1/2.	Base and a part of sides.	Rectangular; 1-3 between chylus cells.	Absent.
<i>P. tenera</i> Eisen.	XV-XVII	Flask shaped; length about twice as long as greatest width.	Apical part almost straight; basal part slightly bent.	Indistinct membrane	Along entire length.	Base and small part of sides.	Rectangular; 1-2 between chylus cells.	Absent.

KEY TO THE SPECIES OF FRIDERICIA KNOWN TO OCCUR IN ILLINOIS.

I. Spermathecae without diverticula -----(An Illinois species not yet described).

II. Spermathecae with diverticula

1. With two diverticula -----+----- (An Illinois species not yet described).

2. With many diverticula around ampulla

a. Setae never more than 4 in a bundle; nine diverticula on ampulla; brain convex posteriorly, concave anteriorly, one and a half times longer than wide; efferent duct of nephridia rises from posterior end of postseptal part-----
--Fridericia agilis Sm.

b. Setae more than 4 in a bundle.

Three to four diverticula on ampulla; no glands at external opening of sperm duct; peptonephridia with many primary and secondary branches; chylus cells in XIII-XVIII-----
-----Fridericia firma nov.sp.

Seven diverticula on ampulla; peptonephridia with many branches rising from common base; two glands at external opening of sperm duct; chylus cells in XV-XVII-----
-----Fridericia tenera nov. sp.

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ABBREVIATIONS USED IN THE PLATES.

A.	-----	ampulla
A.C.	-----	cilia in the apical part of the chylus cell canal.
Al.	-----	anteseptal part of the nephridium
B.C.	-----	buocal cavity
Bh.	-----	branches of the peptonephridium
B.Pn.	-----	basal lumen of the peptonephridium.
Br.	-----	brain
B.S.	-----	blood sinus
C.	-----	cilia
Ca.	-----	chylus cell canal
Cb.	-----	central chamber
Cg.	-----	chloragog cells
Chy.	-----	chylus cells
Cm.	-----	circular muscles
Cu.	-----	cuticula
D.	-----	duct
Dist.	-----	distal
Dl.	-----	dorsal
D.P.	-----	dorsal pore
Dv.	-----	diverticula
E.M.	-----	egg mass in the coelom
E.M'	-----	egg mass about ready to separate from ovary.
Ep.	-----	hypodermis
Eth.	-----	epithelial cells
Ex.	-----	external
Ex. O.	-----	external opening of gland cell
F.	-----	spermiducal funnel
G.	-----	suboesophageal ganglion
GC.	-----	gland cells of the penial bulb
Gd.	-----	guard cells
I.	-----	intestine
I.B.	-----	inner bulb cells
In.	-----	internal
Inv.	-----	penial bulb invagination
I.O.	-----	spermathecal-intestinal opening
L.	-----	lumen
Lin.	-----	lining cytoplasmic layer
Lm.	-----	longitudinal muscles

Ln.-----lining
M. -----mouth
Mu. -----muscle
N. -----nuoleus
Neph. ++-----nephridia
Nf. -----nephrostome
Nv. -----ventral nerve cord
O. -----opening
Oe. -----oesophagus
Ov. -----oviduct
Ovr. -----ovary
P. -----peritoneum
Ph. -----pharynx
Pl. -----penial bulb
P.M. -----penial bulb muscles
Pn. -----peptonephridia
Po. -----penial pore
Pr. -----prostomium
Pro. +-----prolongations of the penial bulb cells
Pst. -----postnephridial part of the nephridia
Px. -----proximal
S. -----setae
Sa. -----septum
Sd.G. -----spermathecal duot glands
Sp. -----spermatheca
Spm. +-----mass of developing sperm in coelom
St', St'', St'''-----first, second, and third septal glands
St. O. -----opening of septal gland duot
Str. -----mid ventral strand of clitellar cells
T. -----'taste' organ
Tr. -----transition from clitellar to bulb cells
Ts. -----spermary
Tu. -----tube muscles
U. -----'free outer surface of the bulb!'
V. -----ventral
Y. -----the so called "yolk substance"
Z. -----mitotic zone in the ovary.

EXPLANATION OF PLATES.

All figures were drawn with the aid of Leitz lenses, oculars no. 1, 2, and 4; objectives 3,5,8, and 1/10 and 1/12 oil immersions.

Fridericia firma nov. sp. figures 1-38.

Fridericia tenera nov. sp. figures 39-50.

- Fig. 1. Lateral view of the anterior region showing shape of the prostomium.
- Fig. 2. One of the anterior setae bundles showing shape, arrangement, and relative sizes. The numbers indicate the relative ages, 1 being the youngest and 6 the oldest.
- Fig. 3. One of the setae showing the shape of the curved proximal end and its lance like distal extremity.
- Fig. 4. The head pore as it appears in a transverse section of the anterior region. X 185.
- Fig. 5. One of the dorsal pores as it appears in a sagittal section of the body. X. 330.
- Fig. 6. Transverse section of the body wall showing structural elements. X 330.
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